of the tarsi ferruginous; abdomen with the apical segment above obscurely, and an irregular oblique streak on each side of the 3rd segment at base a beautiful pale green, the apical two segments are also fringed with a thin white pubescence; wings hyaline and iridescent, nervures and tegulæ testaceous.

♀. Length 12 millim.; exp. 20 millim.

Hab. Kumaon, N. India.

A very beautiful and distinct species, which I have ventured to name after its collector.

EXPLANATION OF PLATE XIX.

Fig. 1. *Pseudagenia Erigone*, sp. nov., ♀.
2. " *artemis*, sp. nov., ♀.
3. *Paragenia argentifrons*, Smith, ♀.
3 *a*. " " " ♂. Outline of intermediate coxa.
4. *Pompilus unifasciatus*, Smith, ♀.
4 *a*. " " " ♀. Head from the front.
5. " *Aliciæ*, sp. nov., ♀.
5 *a*. " " " ♀. Head from the front.
6. *Salius Autolycus*, sp. nov., ♀.
7. " *satelles*, sp. nov., ♂.
8. " *terrenus*, sp. nov., ♀.
9. " *venatorius*, sp. nov., ♂.

On the Tooth-genesis in the *Canidæ*. By H. W. MARETT TIMS, M.D., F.Z.S., Lecturer on Biology and Comparative Anatomy, Westminster Hospital Medical School. (From the Huxley Research Laboratory, Royal College of Science, London.) (Communicated by Prof. G. B. HOWES, Sec. Linn. Soc.)

[Read 7th May, 1896.]

THE main object with which this research was undertaken was to trace the order of cusp-development and the inter-relationships of the various cusps in the teeth of the Canidæ, and to examine into the evidence thereby obtained bearing upon important and interesting problems of Phylogeny.

While this has been the main object, other secondary questions have not been overlooked. These questions may be briefly enumerated as follows:—

(i.) Whether of the upper cheek-teeth, $\underline{\text{pm.}^4}$ or $\underline{\text{m.}^1}$ more nearly approximates to the type tooth, and is therefore safest for the comparison of known forms?

(ii.) Is there a diverse modification of the teeth for opposite ends of the jaw?

(iii.) Is the *Milk* or the *Permanent* dentition the more primitive?

(iv.) Is *Otocyon* primitive in the number and characters of its teeth?

To these questions I have endeavoured to give an answer.

The general character of the teeth of the Common Dog are known to all, and a brief description of these characters is to be found in most text-books of Comparative Anatomy; but, so far as I am aware, no detailed description of the individual teeth in this and other members of the same family has as yet been given.

In 1880 the late Professor Huxley published (7) his well-known monograph "On the Cranial and Dental Characters of the Canidæ." In this paper a classification of the Dogs was proposed, based largely upon certain dental characters, especially size in relation to the basi-cranial axis. He did not touch upon the characters of the individual teeth which bear upon the homologies and inter-relationships of the cusps.

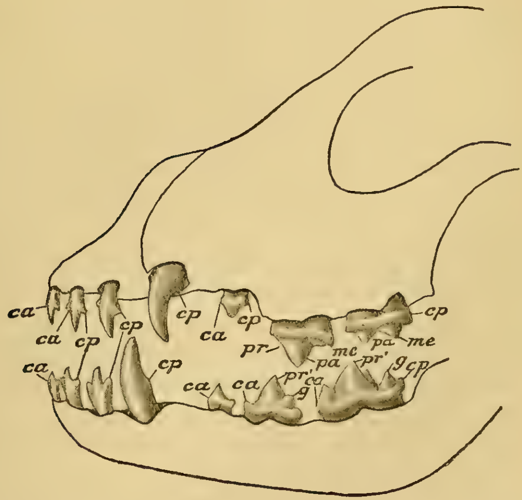
I propose therefore, in the first instance, to give a detailed description of the Milk and Permanent teeth of the Dog. In doing so, I shall employ Osborn's terms, but I shall do so merely as a matter of convenience and not as implying that I thereby accept the Tritubercular theory which he upholds.

Method.—The jaws of animals varying in age from about the seventh week of intra-uterine life up to three months were examined. After being thoroughly dehydrated and clarified in oil of cloves, one side of the jaw was dissected off and the teeth examined *in situ.* The younger specimens were also examined microscopically. The jaws were decalcified in a 1-per-cent. solution of chromic and hydrochloric acids. After staining in borax-carmine, serial sections were cut and models made in wax of some of the developing teeth.

Description of the Milk-teeth.—The dental formula of the deciduous teeth is i. $\frac{3-3}{3-3}$, c. $\frac{1-1}{1-1}$, m. $\frac{3-3}{3-3}=28$. The order and

dates of eruption are as follows :—The first tooth to cut the gum is the lower carnassial ($\overline{\text{dpm.}^4}$), and this is quickly succeeded by the upper ($\underline{\text{dpm.}^3}$). The former just makes its appearance about the end of the second week. By the end of the third week these teeth are well through and $\overline{\text{dpm.}^3}$ and $\overline{\text{c.}}$ are commencing to appear, the former slightly preceding the latter. These are soon followed by $\underline{\text{c.}}$ and $\underline{\text{i.}^3}$, which cut the gum at nearly the same time. $\underline{\text{dpm.}^2}$ appears next, and about the same time $\underline{\text{dpm.}^4}$. These are followed by the remaining upper incisors, and then by the lower incisors. The last deciduous tooth to be erupted is $\overline{\text{dpm.}^2}$, which does not appear until nearly the third month.

Fig. 1.



Deciduous dentition of *Canis familiaris*, seen from the left side. Lettering explained in the text.

Upper Teeth.—The three upper incisors increase somewhat in size from within outwards, but they are all of the same pattern. When viewed anteriorly their crowns may be likened to a "fleur-de-lis," consisting of a main central cone with a small, but well-marked cusp on each of its sides (fig. 1, *ca* and *cp*). On the internal face there is a well-marked cingulum, which is seen to be continuous with these smaller cusps. On comparing the outer with the central incisors, it will be seen that the anterior (inner) cusp has a decided tendency to reduction or non-

development in the former, while the outer (posterior) cusp becomes decidedly more pronounced.

The canines are long, pointed, and recurved; the cingulum is scarcely, if at all, perceptible; the posterior cusp is usually to be recognized, and occasionally, but more rarely, the anterior one also. The cusps may be seen in fig. 1; the anterior cusps are marked *ca* and the posterior *cp*.

The first functional deciduous premolar ($\underline{\text{dpm.}^2}$) is a conical tooth with two fangs. The cingulum is to be made out and in connection with it anterior and posterior cusps; the latter is the more pronounced and lies in the same antero-posterior line as the main cone, while the anterior cusp is placed slightly to the inner side of that line and is quite small.

The second functional deciduous tooth or milk carnassial ($\underline{\text{dpm.}^3}$) is a much larger tooth and considerably more extended in the antero-posterior direction, as will be seen on reference to fig. 1. It bears two external cusps: the anterior, or Paracone (*pa*), considerably the larger, is conical, and its anterior slope is much greater than its posterior. The posterior, or Metacone (*me*), has a horizontal cutting-edge. The cingulum is well-marked along the inner side of the postero-external cusp and at the antero-internal side of the main cone, and in this latter situation is a well-marked cusp, the Protocone (*pr*). This tooth has three fangs—two in the antero-posterior line, as in the tooth in front, and a third sloping inwards and forwards like a buttress. The latter is united to the tooth on the inner face of the main cone, and it is here that the cingulum is deficient.

The third functional deciduous premolar ($\underline{\text{dpm}^4}$) bears two external subequal cusps, the Paracone and Metacone (*pa* and *me*). The cingulum appears to surround these on the anterior, external, and posterior faces, while internally it is well-marked but carried inwards some distance, having a well-marked depression between it and the Paracone and Metacone. This is seen in fig. 3. At its most internal part the cingulum is raised up into a pronounced ridge-like cusp, the Protocone (*ci*).

Lower Milk-teeth.—The description already given of the upper incisors and canine will apply equally well to the corresponding teeth of the lower jaw.

The first functional deciduous premolar ($\overline{\text{dpm.}^2}$) has a prominent conical cusp, the anterior border of which is almost perpendicular. The posterior border has a more decided slope, in the middle of

which is an indication of a cusp. On the inner side is a distinct cingulum, giving rise to well-marked anterior and posterior cusps (*ca* and *cp*), the former lying slightly to the inner side of the main cone, as is the case in the corresponding tooth of the upper jaw.

The *second functional deciduous premolar* ($\overline{\text{dpm.}^3}$) has exactly the same characters, but more pronounced, especially in the case of the cusp (*g*) on the posterior slope of the main cone, which is here of considerable size.

The *third functional deciduous premolar*, or lower carnassial ($\overline{\text{dpm.}^4}$), is a large and massive tooth and of considerable antero-posterior extent. It has a prominent cone about the middle of the external face, the Protoconid (fig. 1, *pr′*), in front of which is the Paraconid (*ca*), the free end of which forms a cutting-edge. Posteriorly is a cusp (*g*) entering into the formation of the so-called *heel*, and separated from the Protoconid by a large depression. The cingulum is marked on the posterior half of the internal face of this tooth; it gives rise to a minute cusp at the postero-external border of the tooth. On the ridge of the cingulum are two well-marked cusps—an anterior Metaconid, the larger, lying at the postero-internal angle of the Protoconid; and posteriorly a smaller cusp.

It will be noticed that I have refrained from applying names to any but the three primary cusps. I have done so, as I am unable to reconcile the cusps of some of the teeth, notably the lower carnassial, with the descriptions usually given. Even the Paraconid (the cusp usually described as the antero-internal), if examined in the lower carnassial, is antero-external, rather than antero-internal.

But, omitting these minor difficulties, is it possible to homologize the all-important Protocone?

I have been unable to find that any attempt has been made by the upholders of the Tritubercular theory to homologize the cusps of the premolar teeth with those of the molars. Scott (23) believes that in the upper *premolars* the protocone forms the antero-external cusp, a conclusion with which, as will be seen below, I entirely agree, and which appears to have been tacitly accepted by Osborn (16 & 17). But these writers do not appear to adopt the view that the main cone of the premolars is homologous with the paracone of the true molars. On p. 443 of his paper cited, Scott states that, "assuming the correctness of

Osborn's results as to the homologies of the molar cusps, those of the premolars are differently arranged."

In consideration of these facts, I would submit the following attempt at identification:—

To start from the upper carnassial tooth, in which there are two external cusps and a very minute antero-internal cingulum-cusp. Following Cope (2), the Paracone and Metacone are defined as the antero- and postero-external cusps, and I think it is justifiable to name the two main cones (fig. 1, *pa* and *me*) of this tooth the Paracone and Metacone. The other very minute cusp must then be the Protocone or antero-internal cusp. It is remarkable that the cone representing *the* primitive reptilian cone should be so diminutive, even allowing with Prof. Osborn (13) that the Paracone and Metacone have undergone "accelerated development."

Turning now to my own identifications in the $\underline{\text{dpm.}^2}$. There is a main cone with its internal cingulum, the latter structure giving rise to a small antero-internal cusp and a somewhat more pronounced posterior cusp lying in the same antero-posterior line as the main cone. I presume that the main or antero-external cone would be regarded by Professors Cope and Osborn as the Paracone, the postero-external cusp, which, as we have seen, is formed by the cingulum, as the Metacone, and the antero-internal cingulum-cusp as the Protocone. If this be so, and I see no other alternative, the Protocone is still more reduced, indeed scarcely perceptible.

In dealing with the canines and incisors there are two alternatives:—

(i.) That there is no internal cusp, and that therefore there can be no Protocone present; or

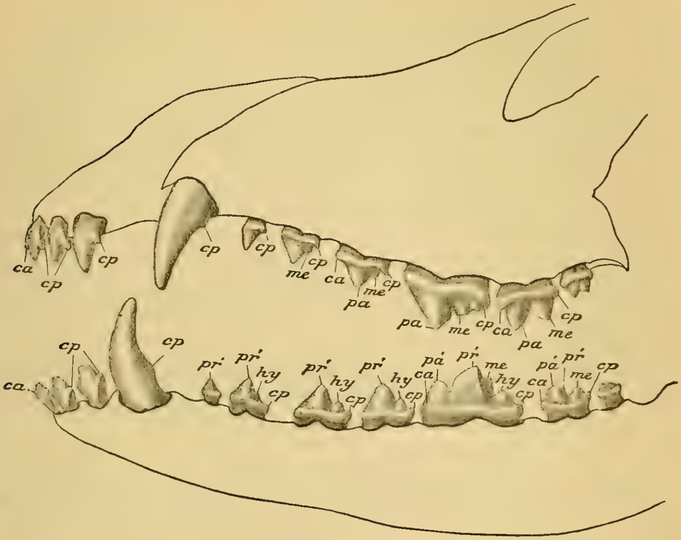
(ii.) That the cusp homologous with the so-called Protocone of the deciduous premolars is the small anterior cingulum-cusp (fig. 1, *ca*).

The latter alternative I believe to be the more probable. If this be so, I think it is trespassing too much upon credulity to regard this minute cingulum-cusp, and not the main central cone, as the primitive cone from which all the others have been derived. Moreover, this cusp is formed by the cingulum, which is itself regarded as a mammalian structure superadded to the reptilian type of tooth; and consequently it is a "reductio ad

absurdum" to derive the remainder of the tooth from this, a structure of admittedly later appearance than the tooth itself.

From this it will be seen that I regard the Protocone of the upper carnassial and the anterior cingulum-cusps of the anterior premolar, the canine, and the incisors as homologous.

Fig. 2.



Permanent dentition of *Canis familiaris*. Lettering explained in text.

Description of the Permanent Teeth of the Dog. (Fig. 2.)

The cusp *hy* is homologous with the cusp inadvertently lettered *g* in fig. 1.

Upper Jaw.—The central incisor has a well-marked central cone and decided lateral cusps, continuous with and formed by the cingulum.

The outer cusp is more distinct than the inner.

i.^{2} possesses the same characters, but is somewhat larger.

i.^{3} is more caniniform. The anterior (inner) cusp (*ca*) is scarcely noticeable, while the posterior is marked and situated nearer to the base of the tooth (*cp*).

All these teeth have well-marked internal cingula continuous with these small cusps.

The *canine* is a long, somewhat compressed, recurved tooth ; the lateral cusps are not so distinct as in the deciduous canine, though the posterior cusp (*cp*) is still to be made out.

The *first premolar* (pm.^{1}) is small and conical, its posterior slope being greater than the anterior. There is a posterior prominence (*cp*), hardly to be called a cusp, into which the well-marked internal cingulum runs. The cingulum

gives rise also to a slight indication of an antero-internal cusp. This tooth has but one fang.

The *second premolar* ($\underline{\text{pm.}^2}$) has two fangs. It is larger than $\underline{\text{pm.}^1}$ but with the same characters more pronounced. In addition there is a minute cusp (*me*) between the main cone and the posterior cingulum-cusp (*cp*).

The *third premolar* ($\underline{\text{pm.}^3}$) has all these characters, but is larger and more pronounced. It is 2-fanged.

The *carnassial* ($\underline{\text{pm.}^4}$) again has the same characters, but the Protocone is proportionately more marked and supported on a separate fang, although very diminutive compared with the other cones.

The *first molar* ($\underline{\text{m.}^1}$) has well-marked Para- and Metacones (*pa* and *me*), the former being slightly the larger. The cingulum is traceable on the external face and becomes prominent at the antero-external angle of the Paracone, in front of which it is continued. At the antero-internal angle at the base of this cone the cingulum divides, both portions being continued backwards separately to the postero-internal angle at the base of the Metacone. On the outer of these two cingulum-ridges rises the well-marked Protocone, between the base of which and the Paracone is a smaller cusp (fig. 3, *d*). At the posterior part of the outer cingulum, immediately behind the Protocone, is another cusp (fig. 3, *i*); the inner cingulum has two cusps placed upon it, as shown in fig. 3, A.

The *second molar* ($\underline{\text{m.}^2}$) has the same characters, but all is much smaller.

Lower Jaw.—The description given above of the upper incisors will apply equally to the corresponding teeth of the lower jaw, with the slight difference that the anterior (inner) cusp is less pronounced in the latter.

Canine. Same as in upper jaw.

Premolars. With the exception of the fact that the cusp (*hy*) situated between the main cone and the posterior cingulum-cusp is better marked, the characters of these teeth are the same as of the corresponding teeth in the upper series.

The *first molar*, or *lower carnassial* ($\overline{\text{m}^1}$.), bears a high main central cone, the Protoconid (fig. 2, *pr'*), with an exceedingly well-marked Paraconid (*pa'*) anteriorly and slightly internal to the Protoconid. Posteriorly to the main cone is the so-called Hypoconid (*hy*), and at the posterior end of this the cingulum forms a small cusp (*cp*). On the inner side of the Hypoconid the cingulum is prominent and terminates anteriorly in the Metaconid (*me*) at the postero-internal angle of the Protoconid. At the postero-internal angle of the cingulum is another marked cusp, the Entoconid, between the base of which and the Metaconid is another small cusp.

The *second molar* ($\overline{\text{m.}^2}$) presents the same characters, with the exception of the absence of the Paraconid and that the Protoconid is scarcely higher than the other cusps.

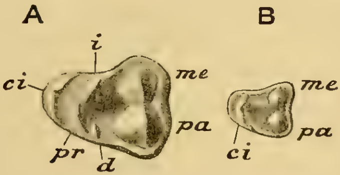
From a consideration of these teeth, the same difficulty in homologizing the Protocone is to be met with as has been pointed out in the deciduous teeth.

On external comparison of the two dentitions certain points are to be noted. In the first place, there is the well-known fact

that the upper permanent carnassial is preceded by a deciduous tooth molariform in character, and that the penultimate deciduous premolar has the *general* characters of the permanent carnassial. The same holds in the lower jaw in relation to $\overline{\text{pm.}^1}$ and $\overline{\text{m.}^1}$.

Again, if the upper milk and permanent carnassials be compared, it will be seen that in the latter *three* external cusps are present, the posterior being the cingulum-cusp, whereas in the former the division of the Metacone into two cusps is not so clearly distinguishable. In the second functional deciduous premolar ($\underline{\text{dpm.}^2}$) there is but the very faintest indication of a second cusp externally, which is very much more marked in its permanent successor. The same thing is to be noted in the lower jaw, but in a lesser degree. From these considerations it will be seen that the teeth of the permanent dentition show an increase both in the number and size of the cusps over the corresponding milk-teeth; in other words, the teeth of the deciduous are simpler than those of the permanent dentition. This fact is still more strikingly shown if the biting-surface of the crowns of the teeth be examined. In fig. 3 is shown the biting-surface

Fig. 3.



A, the biting-surface of First Permanent Molar, and B, of the Fourth Deciduous Premolar of the Dog.

of $\underline{\text{dpm.}^4}$ and $\underline{\text{m}^1}$ of *Canis familiaris*; in the former there are indications of *four* cusps, whereas in the latter *seven* are to be seen.

But this comparison brings out another very important fact. I think it will be generally admitted that the cusp (*pr*) in $\underline{\text{m.}^1}$ is the Protocone; and on comparison with $\underline{\text{dpm.}^4}$ it will be seen that in the latter this cusp, the *Protocone*, is *entirely* absent.

This conclusion I think is very damaging to the Tritubercular theory as I understand it.

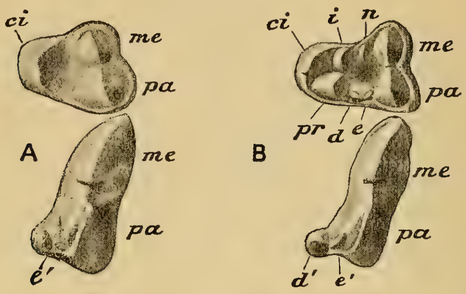
The difficulty in homologizing the Protocone in the various teeth of *Canis familiaris* has already been pointed out, but it is

still further increased by a comparison of the teeth in this Dog with the corresponding teeth in other members of the Canidæ.

If $\underline{\mathrm{pm.}^{4}}$ and $\underline{\mathrm{m.}^{1}}$ of the Jackal (*C. aureus*) be examined and compared, it will be seen that, if any reliance is to be placed upon the homologies of cusps, there is present a very marked difference.

Firstly, there is a large well-marked cusp (fig. 4 B, *pr*) forming

Fig. 4.



A. The biting-surface of the Fourth Premolar and First Molar Teeth of *Cyon rutilans*. B. Similar view of the corresponding teeth of *Canis aureus*.

with the two external cusps (*pa* and *me*) a complete triangle present on the biting-surface of the crown of $\underline{\mathrm{m.}^{1}}$ This cusp is the one, I presume, the Trituberculist would regard as the Protocone. Situated antero-externally to this is a second cusp (*d*), and between this and the Paracone (*pa*) is another small cusp (*e*) placed on a somewhat prominent ridge passing between cusp *d* and the Paracone. On comparing the crown of this tooth with that of the upper carnassial, it would appear that the two cusps (*d'* and *e'*) present on the inner part of the tooth are homologous with the cusps *d* and *e* of the molar tooth, and that the cusp *pr* of the latter tooth, the all important Protocone, is absent entirely from $\underline{\mathrm{pm.}^{4}}$.

If, again, the upper carnassial tooth of *C. aureus* be compared with the corresponding tooth of such a form as *Cyon rutilans*, or even with many examples of the common Dog, it will be seen that the cusp *d'* present in *C. aureus* appears to be absent in *Cyon rutilans* (fig. 4 A), and that the only trace of a cusp on the inner side of $\underline{\mathrm{pm.}^{4}}$ in the latter animal seems to be homologous with the cusp *e'* of the Jackal.

I would here draw attention to the great similarity between

$\underline{\text{m.}1}$ of *Cyon rutilans* and $\underline{\text{dpm.}^4}$ of *Canis familiaris*, a point which will be referred to subsequently. Compare fig. 3 B and fig. 4 A.

It may be urged that the first molar and the fourth premolar belong to an entirely different series, and are not in any way comparable. Such an objection has, I believe, never been raised by any of the supporters of the Tritubercular theory; they have always regarded these teeth as tritubercular derivatives (2), and therefore, I think, one is quite justified in attempting to homologize these various cusps.

If this be allowed, then, I think it must be said that the Protocone of the molars is not represented in the premolars of a form like the Jackal, and that this is still more accentuated in *Cyon*. Consequently, if we are to interpret the anterior premolars in the light of the fourth of the series of the upper *six* cheek-teeth, the *four* premolars would appear to have the all important Protocone wanting.

From these considerations I cannot but think that the greatest doubt is thrown upon the Tritubercular theory by a careful study of the cusps themselves in the various teeth.

Microscopical Examination.

By the discoveries of Flower, Kükenthal, and others the term Monophyodont, in its strictest sense, has become useless, though still employed to designate those animals which have only one *functional* set of teeth.

The Marsupials, the Edentates, and the Cetacea have all histological representatives of at least two dentitions.

In the Dog, indications of three dentitions are to be found, namely, the Milk, Permanent, and Post-permanent; the last being especially well-marked in the region of the third upper incisor of an animal about three weeks old (27). In all the specimens that I have examined, including a fœtus as early as the seventh week, I have been unable to find any trace of a Pre-milk dentition.

Evidences of the Post-permanent dentition have also been adduced by Leche (10) and Kükenthal (8) in the Seal, Röse (21) in Man, and M. F. Woodward (29) in *Erinaceus*. Three dentitions are thus represented in all these animals. The same number is found represented in the Marsupials, but these Leche has referred to a Pre-milk, Milk, and Permanent. He was led thus to regard them from the fact of the functional dentition of

the Marsupials being supposed to be the milk series; and this conclusion was based on the fact that Kükenthal had discovered strong swellings of the dental lamina on the lingual side of these teeth in *Didelphys* (**9**).

In the absence of any evidence of four dentitions being represented in any one part of the jaw of any animal, it seems to me to be only reasonable to infer that the three dentitions of the Marsupials are the same as those represented in the Seal, Man, Hedgehog, and Dog; and, consequently, I would regard Leche's Pre-milk dentition as the vestigial remains of the milk series and the functional set as belonging to the true permanent series, thus reverting to the view long ago held by Flower and Oldfield Thomas. The formerly vexed question as to which is the superadded dentition, the Milk or Permanent, is no longer a serious one, as the three dentitions are an inheritance from polyphyodont ancestors.

The next question arises, to which dentition do pm.[1] and the true molars belong? since they are functional in one series only. If sections of an animal three days old be examined, in the region of the first premolar tooth, three downgrowths of the dental lamina are to be seen, and it is from the central one of these that the tooth develops (**27**). Regarding these three downgrowths as representing the same three dentitions found in the outer incisor region, I would consider this first premolar tooth as belonging to the Permanent or Successional series. This conclusion is, I think, in harmony with that of the majority of observers; but there are some who prefer to regard it as a delayed milk-tooth. This tooth is replaced in one or two animals only, namely, the Indian Taper (**19**), the Hyrax (**3**), occasionally the Pig (**12**) and Rhinoceros, and the extinct Palæotherium (**4**). In these cases the two teeth may be of the milk and permanent, or of the permanent and post-permanent series. I am not as yet in a position to say anything definite upon this point, though, from the appearances of the dental lamina in the Dog and in the Pig, I incline to the latter view.

With regard to the true molar teeth opposing views have also been held, namely, that they are permanent teeth, or that they are delayed milk-teeth. Hoffmann (**6**) has recently concluded that the Ungulate molars belong to the milk series; and Leche (**10**), though admitting that this is by no means settled, is inclined to the same opinion.

If, however, my aforementioned conclusions with regard to pm.[1] be accepted, it must I think be concluded that the molars belong also to the permanent series. If the molar region of a fœtal pup be examined at about the seventh week, the tooth will be seen developing, and there is a slight trace of the dental lamina on its labial side. At a later period, after birth, this labial downgrowth has disappeared, the tooth itself is well developed, and, in addition, there is a strong downgrowth of the dental lamina on the lingual side. Here then, again, are evidences of three dentitions, from the central one of which the molars develop; and, consequently, I regard them as belonging to the permanent series.

Again, it is a very curious but well-known fact that in the upper jaw of the Dog the characters of the last deciduous premolar are similar to those of the first true molar, and those of the penultimate deciduous premolar to those of the permanent carnassial; that is to say, that the specialized carnassial tooth is preceded in position by a tooth molariform in character.

If the last deciduous premolar of a Dog, about three days old, be examined in serial sections, we find a condition identical with that already described in the fœtal condition of the true molar region: namely, a labial downgrowth of the dental lamina, a central one from which this deciduous tooth is developed, and a lingual downgrowth (27). This last downgrowth ultimately disappears, the permanent carnassial developing *anteriorly* and altogether independently of it.

The conditions in the case of this last deciduous premolar being the same as in the case of the true molars, the conclusion must be the same; that is to say, that this deciduous tooth belongs to the same series as the true molars, which it resembles in characters, and that its successor in position, the permanent carnassial tooth, is not its true morphological successor, that successor not developing*.

There here arises the question, to what dentition is the permanent carnassial to be referred? Does it belong to the permanent series; or is it, owing to its great development, a delayed milk-tooth, as my friend Mr. M. F. Woodward has suggested?

In a seven weeks' fœtal pup we find the developing tooth (fig. 5,

* This is in agreement with the conclusion by M. F. Woodward for the Insectivora, in Brit. Assoc. Reports, Ipswich, 1895, p. 736.

pm. 4′) with a *labial* downgrowth of the dental lamina (pm. 4″). I would here digress to remark on the peculiarity of this downgrowth. It assumes at its free extremity a well-marked spherical shape, the epithelial cells becoming concentrically arranged, the central ones having a translucent appearance. It is distinctly connected with the dental lamina. Mr. Woodward tells me he has found a similar structure, in precisely the same situation, in

Fig. 5.—Transverse section through the developing Upper Carnassial of the 7 weeks' fœtal Pup.

Gymnura. I am not able to give an explanation of the condition, but from the facts of its connection with the dental lamina and its presence in precisely the same situation in these forms, I do not think it is a chance structure, and it is possible that it may represent the remains of the predecessor to this tooth which has taken on this peculiar character. The point is, however, I think, worth further investigation.

At a later period in the development of this tooth a well-marked lingual downgrowth of the dental lamina is to be seen, and thus the conditions of its development are identical with those found in the development of the molars.

From these considerations I am of opinion that the upper permanent carnassial does really belong to the so-called Permanent dentition; and that by the great development and extension backwards and upwards of the Metacone the anterior molar has been pushed downwards so as to cut the gum with the milk-teeth.

These facts are of additional interest in that they may afford an explanation of the somewhat similar condition found in some of the Marsupials, in which the posterior premolar alone replaces in position a tooth molariform in character. This deciduous tooth has been regarded as the only one "comparable to the milk-teeth of the Eutheria" (4); and the study of its relationships led Flower and Thomas to regard the functional set of the Marsupials as belonging to the permanent series.

Since Kükenthal's discoveries in the Didelphyidæ (9), this succession has been explained otherwise. The dentition of the Marsupials is now regarded as a persistent milk series, this tooth alone having a permanent successor. I have given reasons above for reverting to the former view; and the fact that this tooth alone is replaced is explained by the entire absence of any functional milk-teeth. I regard this single deciduous tooth as in reality the anterior molar pushed downwards by the overlapping as it were of the premolars and molars at this point, due possibly in the first instance to the gradual shortening of the jaw, and assisted, as in the Carnivora, by the greater development of the Metacone, which by its extension upwards and backwards would tend to force the first molar through the gum. This may be represented diagrammatically in this way:

In cases where the first of the two factors (namely the shortening of the jaw) is alone in operation, the result would be simply to delay the appearance of the successional tooth, as is seen in such forms as *Potorous*; but when the additional factor (namely the extension backwards of the Metacone) comes into play also, the result would be that the deciduous tooth would be shed at an earlier age—that is, it would be accelerated, as is the case in *Thylacinus* and the Carnivora.

The next point of interest in the microscopic examination of

these specimens is whether there is any evidence of the previous existence of additional teeth, and in this connection there are two points which may be mentioned.

(i.) In the incisor region of the upper jaw the dental lamina between $\underline{i.}^{3}$ and $\underline{c.}$ maintains a position extending well down into the substance of the jaw, and does not shorten up as it does between any two of the other teeth. Midway between these

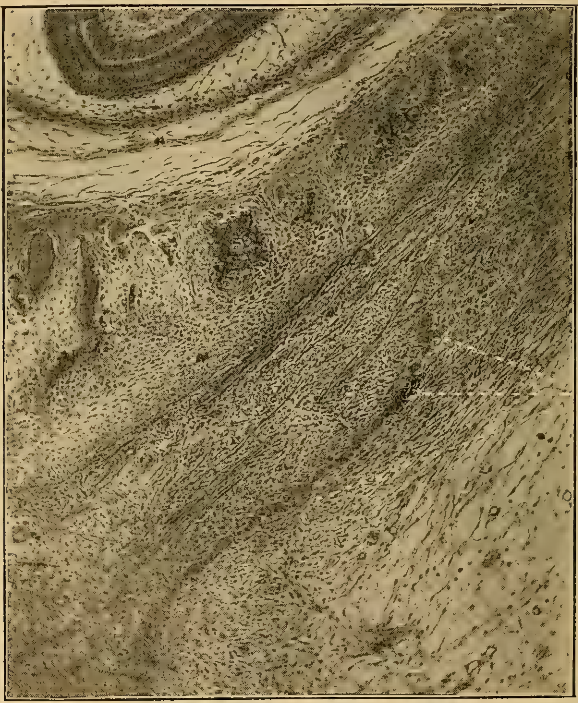


Fig. 6.—Section through the region posterior to the Third Upper Incisor of a 12 hours' Pup, showing apparent vestigial Fourth Incisor.

teeth there is a slight enlargement, somewhat forked (fig. 6, $i.^{4}$), which only extends through a few sections. The position of the dental lamina might be explained by the great development of the canine retaining it deeply in the jaw ; but if it were due to this, one would expect to find the same condition behind the canine as well, which is not the case. It is possible that there is here present the vestigial remains of a fourth upper incisor, though the facts are not conclusive.

(ii.) Behind the last upper molar the dental lamina is continued backwards for some distance; it gets considerably distorted and broken up; but one part of it is more enlarged than the rest. The facts do not allow one to speak with any certainty, but I think it is possible to recognize in it the vestigial remains of a third upper molar, since I can find no trace of such remains in the corresponding position in the lower jaw.

Numerical Variation of the Teeth of the Carnivora.

The number of teeth present in the permanent dentition in living Mammalia varies greatly, and though this variation is somewhat narrower among the Carnivora still it is far from being uniform. This is shown in the accompanying Table (p. 462), which I have compiled from Flower and Lydekker's 'Mammalia,' and certain points, which are worthy of note, may be readily seen.

(i.) *Æluroidea.* The maximum number of teeth present among the members of this group is 40, the Felidæ and Proteleidæ falling as low as 30.

(ii.) *Cynoidea.* The teeth vary from 40 in *Cyon* to 46 or 48 in *Otocyon*; the Canidæ possessing 42.

(iii.) *Arctoidea.* The Mustelidæ have the smallest number (38), while the Ursidæ have 42.

From this it will be seen that the maximum numerical variation is attained among the Æluroidea, the minimum by the Arctoidea, while the Cynoidea occupy an intermediate position; and, moreover, by far the greater number of its members have the same number of teeth, 42. This, I think, justifies the well-established deduction that the ancestral form had 42 or more teeth. It was also probably Pentadactyloid and Plantigrade. These three characteristics are present among the living Ursidæ.

To effect the numerical variations one of two things must have happened—(i.) either teeth must have, in some instances, been superadded, causing an increase in the number; or (ii.) some teeth must have become suppressed. I think the balance of evidence is decidedly in favour of the latter, for the following reasons:—

(i.) Supernumerary teeth, of which examples are given by Bateson (1) in his book 'Materials for the Study of Variation,' are very rare; and the number is never in excess of that found among fossil forms, and may be regarded as "reversions to a

Table I.

Giving a General Survey of the more typical Dental Formulæ of the Carnivora.

CARNIVORA VERA.

- **Æluroidea** ...
  - (α) *Felidæ.* $\frac{3\,1\,3\,1}{3\,1\,2\,1}=\mathbf{30.}$
  - (β) *Viverridæ.* $\frac{3\,1\ (3 \text{ or } 4)\ (1 \text{ or } 2)}{3\,1\ (3 \text{ or } 4)\ (1 \text{ or } 2)}$
    - (i.) *Cryptoprocta.* $\frac{3\,1\,4\,1}{3\,1\,4\,1}=\mathbf{36.}$
    - (ii.) *Viverrinæ.* $\frac{3\,1\,4\,2}{3\,1\,4\,2}$ ($\frac{1}{2}$ m. in *Prionodon*)$=\mathbf{40.}$
  - (γ) *Proteleidæ.* i. $\frac{3}{3}$, c. $\frac{1}{1}$, p.+m. $\frac{4}{3 \text{ or } 4}=\mathbf{30}$ or $\mathbf{32.}$ Premolars and molars very small and simple.
  - (δ) *Hyænidæ.* $\frac{3\,1\,4\,1}{3\,1\,3\,1}=\mathbf{34.}$ Some fossil forms have m. $\frac{1}{2}$ or $\frac{2}{2}$.
- **Cynoidea** ......
  - (α) *Canidæ.* $\frac{3\,1\,4\,2\text{–}3}{3\,1\,4\,2\text{–}4}=\mathbf{40\text{–}44.}$
  - (β) *Cyon.* $\frac{3\,1\,4\,2}{3\,1\,4\,2}=\mathbf{40.}$
  - (γ) *Otocyon.* $\frac{3\,1\,4\ (3 \text{ or } 4)}{3\,1\,4\,4}=\mathbf{46}$ or $\mathbf{48.}$
- **Arctoidea** ......
  - (α) *Ursidæ.* $\frac{3\,1\,4\,2}{3\,1\,4\,3}=\mathbf{42.}$
  - (β) *Procyonidæ.* $\frac{3\,1\,4\,2}{3\,1\,4\,2}=\mathbf{40.}$
  - (γ) *Mustelidæ.* $\frac{3\,1\,4\,1}{2\text{–}3\,1\,4\,1\text{–}2}=\mathbf{36\text{–}33.}$

regularity" (*Darwin*); while examples of numerical reduction are comparatively common.

(ii.) Embryology has brought to light the presence of vestigial remains of additional teeth. Such examples have been furnished by Oldfield Thomas (26) and M. F. Woodward (30) among Marsupials, and I have already given reasons for believing that the same are probably present in the Dog.

One has only to look at such a table as that accompanying Oldfield Thomas's (26) paper to see how very general is such a suppression.

(iii.) Palæontological evidence shows that a large number of Mesozoic Mammals had a greater number of teeth than the majority of those living. That the tendency to the suppression of teeth has been in operation in past ages is amply testified by Osborn (14) in his paper "On the Structure and Classification of the Mesozoic Mammalia." In this paper he gives the dental formula of the primitive heterodont Mammalia as i. 4, c. 1, pm. 4, m. 8 (p. 249); and he goes on to say, "Reduction of this formula was effected by the loss of the lateral incisors, resulting possibly from the hypertrophy of the adjoining canine; the premolars were reduced by regular antero-posterior suppression, or by the loss of the first or second member of the series; the molars were reduced either by antero-posterior or by postero-anterior reduction or by simultaneous reduction of both ends of the series."

And (iv.) if the Mammalia are descended from Reptilian ancestors, as is generally believed, then certainly a reduction in the number of teeth, as well as in the number of dentitions, must have taken place.

From these reasons it is possible to conclude, other things being equal, that the member of a mammalian group which has the greatest number of teeth retains, in that particular, the more primitive condition. If this be so, then I think we must regard the Ursidæ among the Arctoidea, the *Viverrinæ* (with the exception of *Prionodon*) among the Æluroidea, and *Otocyon* not only among the Cynoidea, but among the whole Carnivora, as retaining the most primitive condition as to the number of their teeth, which in the last-named genus is 46 and in one specimen 48. That *Otocyon* is in this respect the most primitive, among the Cynoidea, was a view long ago held by Huxley (7).

Cope, in his paper "On the Mechanical Origin of the Sectorial Teeth of the Carnivora" (2), remarks "it is well known that in the evolution of the sectorial dentition of the Carnivora the number of molars and premolars has considerably diminished."

It has been said (4), in connection with the primitive dentition of *Otocyon*, that "there is at present no palæontological proof of this, as none of the numerous fossil forms of Canidæ yet discovered have more than the normal number of molars." I would point, in answer to this, to such a form as the Oligocene *Daphænus* with a dental formula $\frac{3\,1\,4\,3}{3\,1\,4\,3} = 44$, which, according to W. B. Scott (24), is in the direct line of ancestry of the Dog. This genus differs from the specimens of *Otocyon*, with the single exception above referred to, in the loss of one lower molar only. If we look at all the members of the Carnivora in which the number of molars is not equal in both jaws, it will be seen that the number is always greater in the lower jaw, from which one might infer that the upper molars were the first to undergo numerical reduction; and from this it follows that, given an equal number of true molars in both jaws, if any teeth have undergone suppression, the last tooth to have been suppressed would be in the lower jaw. If this inference be allowable, then we may presume that one of the more immediate ancestors of *Daphænus* had an additional lower molar, the loss of which alone distinguished it from *Otocyon*.

That the Canidæ very early acquired a reduced dentition is a fact, and it is, I think, in accordance with their great number and wide distribution both at the present time and in past ages; and, conversely, the retention by *Otocyon* of a primitive dentition agrees with its restricted area of distribution, one species (*O. megalotis*) only being known.

From these considerations I am the more inclined to the opinion that in *Otocyon* we have to do with a form in which a very primitive numerical condition of the teeth has been retained.

Description of the Permanent Teeth of Otocyon megalotis.

Upper Jaw.—The first and second incisors are very similar to those of the Dogs generally. Between the $\underline{\text{i.}^2}$ and $\underline{\text{i.}^3}$ is a slight diastema.

The *third incisor* is somewhat larger than the others. It has a cingulum on

its internal face which runs upwards, at the margins of the tooth, to the apex of the crown. Between this tooth and the canine is a wide diastema.

The *canine* is long, pointed, and recurved, and shows a similar condition of the cingulum on its internal face. Between this tooth and $\underline{\text{pm.}^1}$ is a very wide diastema.

The *first premolar* is much reduced and with but a mere trace of an internal cingulum. The posterior margin of the tooth shows a slight angulation which in the more posterior premolars appears as a minute cusp. Between this tooth and $\underline{\text{pm.}^2}$ is a distinct diastema.

The *second premolar* is rather larger than the first and has two fangs. A minute cusp is to be seen at the posterior border formed by the internal cingulum which runs into it. The cingulum is also more noticeable on the inner face of the anterior root; that is, in the position of the Protocone.

Slight diastema between $\underline{\text{pm.}^2}$ and $\underline{\text{pm.}^3}$

The *third premolar* has characters similar to those of the second but more marked, as it is a somewhat larger tooth.

The *fourth premolar* has a main cone with a well-marked cusp anteriorly and another posteriorly to it. There is a very well-marked ridged cingulum on the internal face of the main cone, which leads up to and forms the anterior and posterior cusps. The Protocone is large, almost as high as the main cone, and placed in the same transverse line. *It is distinctly a cingulum-cusp.*

On the ridge of the cingulum, leading from the Protocone to the posterior cusp, is another small cuspule placed somewhat nearer to the Protocone. On the posterior slope of the main cone of the tooth is seen a minute cusp, distinct from the posterior cingulum-cusp, which is, however, more marked in $\overline{\text{pm.}^4}$. A slight trace of the cingulum can be seen on the outer face of $\underline{\text{pm.}^4}$.

The *first molar* has two external cusps of about equal size. The cingulum is seen anteriorly and posteriorly to these and also slightly on the external face, especially of the anterior cusp (Paracone), where it becomes continuous with the Protocone. The cusp situated between the Protocone and the posterior part of the cingulum (seen in miniature in $\underline{\text{pm.}^4}$) is well-marked.

Internally to this again is a secondary cingulum, upon which is placed a pronounced postero-lingual cusp, in front of which the secondary cingulum shelves downwards and forwards; it then bifurcates, one part running into the Protocone, the other passing round in front of it to fuse with the primary cingulum, externally to the Protocone.

The *second molar* has similar characters to $\underline{\text{m.}^1}$, but the Paracone is higher and more pointed than the Metacone.

The *third molar* is of the same pattern but is a smaller tooth, and therefore the individual cusps are not so clearly differentiated.

Lower Jaw.—Incisors small and more procumbent than in the Dogs generally. All are about equal in size.

No diastema between $\text{i.}^{\overline{2}}$ and $\text{i.}^{\overline{3}}$.

The *third incisor* has a well-marked internal cingulum rising into two small cusps at its extremities, but from the position of the tooth they lie more on the internal face than laterally.

Practically no diastema between $\overline{\text{i.}^3}$ and $\overline{\text{c.}}$

The *canine* is smaller than $\underline{\text{c.}}$ Internal cingulum present.

The *first, second, and third premolars* possess similar characters to the corresponding teeth in the upper jaw, with the addition that in $\overline{\text{pm.}^3}$ the anterior cingulum-cusp is more pronounced.

The *fourth premolar.* The main cusp has a well-marked secondary cusp on its posterior slope. The cingulum is not very distinct in the middle of the inner face of the main cone; but anteriorly it gives rise to a cusp, and posteriorly, where it becomes broader and more prominent, it forms two small cusps which are situated transversely side by side.

First molar. Outer surface. Two cusps are to be seen, an antero-external (Protoconid), which is higher and stronger than the postero-external (Hypoconid).

Inner surface. Two cusps also, an antero-internal (Metaconid) and a posterior (Entoconid) cusp, the former being the higher.

Anterior surface. The Paraconid, which has more of the character of a transversely elongated ridge than a cone.

Posterior surface. The cingulum is to be traced around the bases, posteriorly, of the Entoconid and Hypoconid, and opposite the interval between these two cusps is the Hypoconulid, placed on the cingulum.

At the antero-external angle of the tooth is a small secondary cingulum, which becomes lost upon the anterior surface of the Paraconid.

The *second molar* has the same pattern as the first, the differences being that the Metaconid is more developed than the Protoconid; the Paraconid is more pronounced than in $\overline{\text{m.}^1}$.

The secondary cingulum at the antero-external angle of the tooth is more marked and bears a cusp, in consequence of which the Protoconid appears to lie more towards the middle (antero-posterior) line of the tooth.

The *presence of this cusp on the external cingulum* is a fact upon which I wish to lay stress, and to which I shall again refer.

The *third molar* has the same characters, but smaller. Paraconid still more reduced.

The *fourth molar* is much smaller. Paraconid scarcely visible.

I have given reasons above for believing that *Otocyon* is primitive in respect to the number of its teeth, and I think it will readily be admitted, from a consideration of the teeth themselves, that they possess decidedly multituberculate characters. The question once more arises, Is this multituberculate condition primitive or not? The consideration of the answer to this question has an important bearing upon the theory of the multituberculate origin of the Mammalian teeth, as put forward by Forsyth Major (**11**), and supported by Goodrich (**5**) and others.

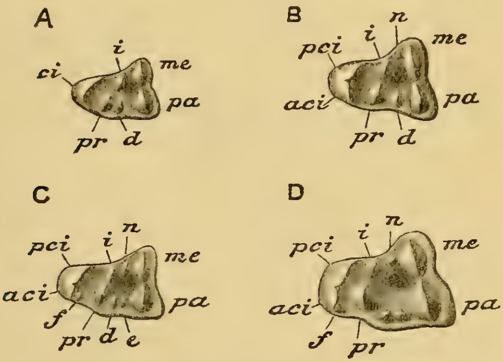
In dealing with this question it is necessary to here examine the teeth of various species of Dogs. This I have had an oppor-

tunity of doing through the kindness of Mr. Oldfield Thomas, to whom my best thanks are due for having allowed me to have free access to the specimens in the British Museum. In carrying on this part of my investigation I have taken Huxley's monograph, "On the Cranial and Dental Characters of the Canidæ" (7), as my guide.

In this paper Huxley divided the Canidæ primarily into two series, the Thooid and Alopecoid, and arranged several of the members in each series in a fairly definite order of specialization, distinguishing the Macrodont from the Microdont forms.

It will not be necessary to take each member of the series individually. Commencing with the Thooid series, it will be sufficient to examine *C. Azaræ* (817 A), *C. cancrivorus* (46. 1. 28. 57), *C. magellanicus* (184 *b*), *C. anthus* (816 *a*)*.

Fig. 7.



The biting-surface of the First Right Upper Molar Tooth of—A. *Canis Azaræ*; B. *C. cancrivorus*; C. *C. magellanicus*; D. *C. anthus*. (Thooid Series.)

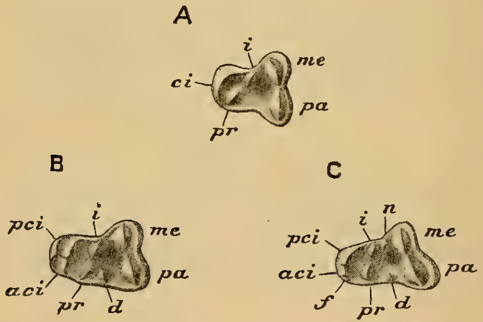
Fig. 7 delineates the crown of the *first right upper molar* in each of these forms. *C. Azaræ* (A) and *C. cancrivorus* (B) belong to the Microdont series, and have the fewest cusps, the former having *six* and the latter *eight*; whereas *C. anthus* (D) (which with *C. aureus* belongs to the Macrodont series) has ten cusps. The measurements of *C. magellanicus* (C) appear to vary, but working out the measurements given by Huxley (*op. cit.* p. 267), it

* These numbers refer to the particular British Museum specimens from which the drawings were taken.

also would certainly belong to the Macrodont series and it has likewise *ten* cusps. The same increase in the number of cusps may be seen in the lower carnassial teeth in members from opposite ends of the series. I would also draw attention to the increase in size of the external cingulum in passing up the series; indeed, in *C. anthus* it forms a projection at the antero-external angle of the tooth, nearly half the height of the Paracone itself. This I regard as an important point, as I have already shown that cusps are formed on it in *Otocyon*. The same condition is also to be seen in some of the Insectivora—a condition which, I believe, should necessitate reconsideration of the interpretation of the cusps in some of those forms which are regarded as having typically tritubercular teeth.

The same increase in the number of cusps may be noted in the Alopecoid series. In fig. 8 are shown the biting-

Fig. 8.



The biting-surface of the First Right Upper Molar tooth of—A. *Canis littoralis*; B. *C. niloticus*; C. *C. lagopus*. (Alopecoid Series.)

surfaces of the first right upper molar of *C. littoralis* (*C. virginianus*, Mivart) (88. 11. 25. 2), *C. niloticus* (56. 3. 12. 14), and of *C. lagopus* (88. 2. 20. 12). *C. littoralis* is one of the lower Microdont Alopecoid dogs, while the two latter belong to the Macrodont series, and in these more cusps are present than in *C. littoralis*.

This conclusion has been arrived at after a very careful study of the large number of skulls of the Canidæ preserved in the British Museum. In some cases the teeth were too worn to afford very reliable information; I was therefore led to select

individual skulls, in which the tooth-cusps were more complete (*i. e.* least worn), for special illustration, but the general conclusion was in entire accordance with the view just stated.

The outcome of these considerations, with regard to *Otocyon*, is—that it is primitive in respect to the number, but specialized in respect to the multituberculate condition of its teeth.

These conclusions are apparently in direct contradiction to those arising out of the study of the genus *Cyon*. The members of this genus are distinguished from the true Dogs chiefly by the loss of the last lower molar. I have already drawn attention to the fact of the great simplicity of $\underline{\text{m.}^1}$ of *Cyon rutilans*, a tooth more primitive even, according to my views, than $\underline{\text{dpm.}^4}$ of the Dog.

I am not in a position to do more than suggest, as a possible explanation, that the genus *Cyon* became separated off from the true Dogs at an early period, and that its teeth, while retaining the simplicity of their crowns, have undergone numerical reduction. These animals also differ from the ordinary Wolves, Jackals, and great majority of domestic Dogs, according to Huxley (7), in the breadth of the jaws and the convexity of the facial line. I would emphasize the great resemblance which exists, both in the number and pattern of the teeth, between the members of this genus and *Viverrinæ*, as tending to the suggestion that they have all descended from a common stock, early separated from the true Canidæ.

Embryological Evidence as to the order of Cusp-development.

The value of evidence of this nature is based upon the assumption that Ontogeny recapitulates Phylogeny. Of course this assumption may be doubted, but it is interesting to note that Osborn, a great upholder of the tritubercular view, believes in it strongly, as may be gathered from the following. In an address "On the History of the Cusps of the Human Molar Teeth," delivered before the New York Institute of Stomatology in April 1895 (15), occur the following words:—"We should expect, in the embryonic jaw, that the calcification of the tooth-germ would be very significant, because we know that the embryonic structures in their development follow the order of addition or evolution." Having made this definite statement, in the next sentence he makes a partial retraction by saying, "The order of

evolution is, *to a certain extent*" (the italics are mine), "repeated in embryonic development." However, we can gather from this that Osborn admits the validity of the assumption.

Upon this basis, let us see how the facts may be reconciled with the tritubercular theory. According to this, the Protocone should be developed first, and the Paracone and Metacone almost simultaneously but at a later period, and the talon, or heel, still later. This is the order in which the various cusps have arisen, according to Prof. Cope (2); consequently this is the order in which they should appear ontogenetically.

The cusp-development has been worked out by Röse (22) in the Primates and Marsupials, and by Taeker (25) in the Ungulates. Their results are seen in the accompanying Table (II.), copied

TABLE II.

UPPER MOLARS.

	Primates.	*Marsupials.*	*Ungulates.*	
1.	Paracone.	Paracone.	Paracone.	1.
2.	Protocone.	Protocone.	Metacone.	2.
3.	Metacone.	Metacone.	Protocone.	3.
4.	Hypocone.	Hypocone.	Hypocone.	4.

LOWER MOLARS.

1.	Protoconid.	Protoconid.	Protoconid.	1.
2.	Metaconid.	Paraconid.	Metaconid.	2.
3.	Hypoconid.	Hypoconid.	Hypoconid.	3.
4.	Entoconid.	Entoconid.	Entoconid.	4.
5.	Hypoconulid.	Metaconid.		

from a paper by Osborn (13), and with them my own results, as seen in the Dog, are in agreement. From a study of this table the most striking fact is revealed that while in not one of the four orders does the Protocone develop first, the Protoconid does so in every instance. This is a very important point.

In the above-mentioned address by Osborn (15), the fact of the agreement in the lower jaw and disagreement in the upper jaw is thus referred to; he says:—"In the lower molar teeth the order of calcification is precisely the order of evolution;" and after dealing with this order of development, he goes on to say: "So we find that the order of embryonic development exactly repeats the order of historical development, and in every way presents the strongest kind of confirmation of the theory of cusp-formation which we have been discussing." He omits to mention that the Paraconid does not develop at all.

Of course Osborn is dealing here with the human teeth only: otherwise, if he were dealing with the Marsupials as well he could hardly be so satisfied, for in these the Metaconid, instead of developing almost simultaneously with the Paraconid, does not appear until after the Hypo- and Entoconid.

In the same address, in dealing with the upper jaw, Osborn says so little, that I may quote it all:—"But this, you see, is not exactly the case in the upper molars. Nevertheless, out of eight cusps in the upper and lower molars considered together, *six* cusps calcify in the order in which they were successively added to the single reptilian cone." Surely this representative of the reptilian cone is *the* important one, and the fact that it does not develop first in any one of these four orders is a point not easily to be explained away.

Again, it appears to me that Osborn gives undue weight to the lower jaw, almost ignoring the upper, which does not fit in with his views. I would point out that in the Canidæ the secondary cusps are better developed in the teeth of the lower jaw than in the corresponding teeth of the upper, both in the milk and permanent dentitions; and I have already pointed out that the more primitive the teeth the fewer the cusps: consequently, it follows that the teeth of the upper jaw retain more of the primitive character than do those of the lower. Hence, if reliance is to be placed on the cusp-development of the teeth in one jaw over those of another, it is the upper jaw which, to my mind, should be selected, and not the lower.

From a consideration of the results obtained by investigation into the embryological history of the cusps, I think it must be admitted that Osborn's conclusions are not borne out, but are, on the contrary, disproved, and this by the very kind of evidence upon which he places reliance.

There are still other objections which may be urged against the Tritubercular theory. The upholders of this view assume that there has been a rotation of the Paraconid and Metaconid inwards in the lower jaw and outwards in the upper, giving rise to the Tritubercular as opposed to the Triconodon type of tooth. A great objection to this has been put forward by E. S. Goodrich (5), who points out that there is no evidence whatever of any traces of the beginning of the movement of cusps from the Triconodont to the Tritubercular form.

It may be as well to summarize the arguments which may be now urged against the Tritubercular theory:—

(i.) That in not one of the four orders, Marsupials, Ungulates, Carnivora, or Primates, does the Protocone develop first.

(ii.) That in *two* out of the four orders it does not even develop second, being preceded by the Metacone.

(iii.) The frequent absence of the Paraconid.

(iv.) That in the Marsupials the Metaconid, which, together with the Paraconid, is second in importance only to the Protoconid, is developmentally preceded by the Hypoconid and Entoconid.

(v.) That if the homology of the cusps which I have already attempted to give be correct, it follows that the Protocone is absent from all the teeth of the Canidæ, and, I think it may be added, from all the teeth of the Carnivora, with the exception of the true molars.

(vi.) That the Protocone is absent from the molariform $\underline{\text{dpm.}^4}$ of the Dog, a tooth of exceedingly primitive characters.

(vii.) The absence of the Protocone from the $\underline{\text{m.}^1}$ of such a form as *Cyon rutilans*, this tooth, as I have already pointed out, having characters very similar to $\underline{\text{dpm.}^4}$ of the Dog.

(viii.) The absence of any evidence of the commencement of the movement of rotation of the cusps, such as is presumed to have taken place; and

(ix.) The existence of the Multituberculata at such an early geological period.

In addition to these, several very weighty objections have been forcibly urged by Dr. Forsyth Major in his paper on the Miocene Squirrels (**11**).

Another theory to account for the tooth-genesis of the Mammalia is that which was advanced by Forsyth Major (**11**), and supported by Goodrich (**5**) and others, and is known as the Multitubercular theory.

These authors would derive all teeth from the Multituberculate type; but I think there are strong objections to this view also, for the following reasons:—

(i.) This view does not attach any special importance to any one cusp over another; and yet we find that the antero-external cusp always develops first both in the upper and lower jaws, the other cusps being added subsequently in a more or less

definite order, and not that several cusps appear at first and subsequently some become suppressed.

(ii.) All the fossil Multituberculata have a specialized dental formula with numerically reduced incisors and no canines: consequently I am unable to believe that the Carnivora and Insectivora, with their full dental formulæ, have been derived from these.

(iii.) That there is a progressive increase in the number of cusps in both the Thooid and Alopecoid series of Dogs, in passing upwards from the more primitive forms.

(iv.) That the teeth of the deciduous dentition are more primitive than those of the permanent and have fewer cusps.

(v.) Goodrich remarks that "Multituberculate forms increase in number the lower we search:" this increase, of which I am unable to convince myself, must be very small, and the total number found at present is greatly below that of non-multituberculate forms, and of equal, but not greater antiquity.

Such forms as *Otocyon*, which I consider to be primitive in the number of its teeth, have, I believe, secondarily acquired the multituberculate condition. The Monotremes may be directly descended from the Multituberculata, as may also such orders as the Rodentia with their specialized dental formulæ, though, as I have not specially worked at this point, I am not in a position to express a more definite opinion.

Having thus seen that neither the Tritubercular nor the Multitubercular theory satisfactorily explains the origin of the teeth of the Carnivora, the question naturally arises, Is there any alternative theory that may explain it? I venture to think there is.

In the first place, the history of the development of the cusps shows that the antero-external cone is the first to develop, both in the upper and lower jaws, in all four of the orders to which I have referred. This uniformity cannot be without significance, and I think one must regard this cone as the representative of the primitive reptilian cone*: in other words, I would regard the Paracone and Protoconoid as homologous cusps, and to avoid confusion I would term this the primary cone. The

* This conclusion appears to be in accordance with the views of Winge (28. From his illustrations he appears to regard the Paracone as homologous with the Protoconid, and the Metacone with the Hypoconid.

next structure to which I attach great importance is the internal cingulum. We have already noted its constant presence. That it is a structure of great antiquity is proved both embryologically and palæontologically. If the teeth of a fœtal pup be examined the cingulum is, proportionately to the primary cone, much larger than in the fully-developed tooth. It is also present in some of the fossil Mammalia of the Stonesfield Slate (5); as, for example, *Amphitherium*. The ends of this internal cingulum, which is generally regarded as a mammalian characteristic, give rise to the small anterior and posterior cusps, such as we have seen exist in the incisor teeth of the Dog. Such a form of tooth at once suggests that of the fossil *Microconodon*. In the more specialized cheek-teeth the cingulum, though always more marked internally, is continued round the external face of the tooth, and, as we have seen, may give rise to cusps externally, as in *Otocyon* and possibly some of the Insectivora.

This description of a tooth with a main cone and small anterior and posterior cusps agrees with the description of the premolars of *Amphitherium Prevostii* given by Owen (18). These teeth, he says, "consist of a single compressed conical cusp with a minute tubercle at the hind part of its base and a more minute one in front." We have already seen that in the teeth of the Dog the posterior cingulum-cusp is usually more marked than the anterior. Goodrich (5), in describing the British Museum specimen of *A. Prevostii*, which he has fully exposed, says (p. 414) that the premolars have "a laterally compressed crown bearing one large cusp, a very small anterior cingulum-cusp, and a posterior heel."

The anterior cingulum-cusp does not usually undergo further development. In certain cases, however, in which it does do so, it may form an anterior cone, thus giving rise to a Triconodont tooth. The only teeth in the Dog in which it undergoes development are the deciduous and permanent lower carnassials, giving rise to the cusp usually termed the Paraconid. In these teeth the cingulum runs right up into that cusp, and does not extend forwards as is the case at the posterior end of the tooth. This anterior cingulum-cusp is placed somewhat to the inner side of the primary cone, giving rise to the Protocone of the upper premolars of the Dog and the Paraconid of the lower carnassial.

The posterior cingulum-cusp is usually well-marked, and in

the upper carnassial of the Dog forms the posterior part of the Metacone, and in the lower the posterior (smaller) part of the Hypoconid. Consequently, it will be seen that the *talon* of the lower carnassial appears very early. This is in accordance with the early appearance, geologically, of the trituberculo-sectorial type of tooth. Moreover, Forsyth Major (**11**) asserts that the talon, though reduced, as compared with the rest of the tooth, in the Carnivora, is well developed in all other orders—therefore, *à priori*, it is not a late development; and he also points to the fact that several Archaic Eutheria, including some Creodonta from the Cernaysian fauna of Rheims, have a more distinctly marked talon than in many later forms, both in longitudinal extension and in height of cusps. Again, Goodrich affirms (**5**) that we must conclude that the common ancestors of both Placentals and Marsupials possessed this (trituberculo-sectorial) type of tooth.

Following upon this, the next structure to be added is what I propose to term the *Secondary Cone.* It arises upon the posterior slope of the Primary cone, and is of mechanical origin due to contact with the Primary cone of the opposite jaw. This cone is seen in its most rudimentary form in the anterior premolars of the Dog. The more it becomes developed the more the opposing cusp would tend to wedge it backwards and separate it from the Primary cone from which it has been developed. This cone forms the anterior part of the Metacone of the upper carnassial, and the Metacone of the upper true molars. In the lower carnassial it forms the anterior, larger portion of the talon, and postero-external cusp of $\overline{\text{m.}}^{2}$. This cusp only develops, to any extent, in the premolars of those forms whose dentition approximates to the Carnivorous type.

Upon the internal cingulum there develops a Centro-internal cusp, situated slightly posteriorly to the middle of the antero-posterior line of the tooth. This cusp is not developed in the premolars of the Canidæ. It forms in the molars the cusp *ci* (fig. 3, B) and gives rise to the Metaconid of the lower carnassial.

As the upper jaw comes to overlap the lower, the opposing cusps would so interlock that the internal cingula of the molars would tend to be wedged inwards away from the main mass of the tooth; the depression thus formed, other cusps would tend to be formed, giving rise to those marked *pr* and *i* in the same figures.

With regard to these smaller cusps it is difficult to express any opinion as to the precise order of evolution, as the results, both palæontological and embryological, are at present somewhat conflicting.

It will be noticed that I have reserved the term *Cone* for that which I regard as the representative of the Reptilian tooth and to its secondary derivative; while the term *Cusp* I have applied to the remainder, all of which I regard as having been developed upon the cingulum.

Table III. gives the order of evolution of the cones and cusps according to this view, and also the cusps with which they correspond, according to the system of nomenclature now in vogue. It will be readily understood that it is impossible fully to deal with this question in a small space, as, from what I have attempted to show above, cusps bearing the same name in different teeth, and even the same teeth in different species, are in reality not homologous. I have therefore confined myself almost entirely to a consideration of the teeth in the Canidæ.

Table III.

Showing the order of development of the Cusps according to the Theory of Cingulum-cusp Development and the Cusps which they represent in the Upper and Lower Jaws of the Dog.

1. Primary Cone	Paracone.	Protoconid.
2. Anterior Cingulum-cusp.	Usually remains minute; forms the Protocone of the upper premolars.	Remains minute in all except the lower carnassial, in which it forms the Paraconid.
2. Posterior Cingulum-cusp.	Forms posterior part of the Metacone.	Minute. Enters into the formation of the Hypoconid at its posterior part.
3. Centro-Internal Cingulum-cusp.	Absent in the premolars. Forms the Protocone of $\underline{\text{dpm.}^4}$ and the *heel* of $\underline{\text{m.}^1}$.	Absent in premolars. Forms Metacoid.
4. Secondary Cone ...	Anterior part of Metacone in the premolars and almost the entire Metacone in the molars.	Anterior part of the Hypoconid and postero-external cusp of molars.

Having thus given a brief outline of what may be termed a Theory of Cingulum-cusp development, it is necessary to examine how far such a theory is borne out by Palæontology and Embryology.

(i.) *Palæontological evidence.*—Starting from the Haplodont

cone, the next form would be that of a tooth with a main central cone and minute lateral cusps. Such teeth are to be found in *Micoconodon.* The prominence of the Internal Cingulum with the formation of a central cusp upon it is clearly to be seen in such teeth as those of *Amphitherium Prevostii* and *Peraspalax*; whilst the presence of the Secondary cone is to be noted in the molar teeth of almost all forms. From the consideration of such forms as these, I think it is evident that Palæontology furnishes quite as strong evidence in favour of such a theory as I have attempted to describe, as it does for either the Tritubercular or Multitubercular theory.

(ii.) *Embryological evidence.*—The strongest confirmation of this view is to be found in the fact that in all the orders in which the cusp evolution has at present been worked out, the Primary cone (Paracone and Protoconid) develops first in every instance, in both upper and lower jaws.

That the Cingulum is a structure of great antiquity and importance is borne out by the fact that it appears developmentally very shortly after the Primary cone can be distinguished. In the teeth of the fœtal Dog it is comparatively very largely developed, especially in the incisors. The internal cingulum is more marked in the lower members of both the Thooid and Alopecoid series than it is in the higher; and its presence, together with the small anterior and posterior cingulum-cusps to which it gives rise, is to be noted in all the teeth of the Dog, both milk and permanent. So far this theory is in accordance with all known embryological facts; the difficulty arises in connection with the secondary cusps. To explain my meaning more fully: if the development of the cusps of $\underline{\text{dpm.}^{4}}$ be traced, the so-called Protocone of that tooth commences to appear before the Metacone, though the latter soon surpasses it in size; this result agrees with those of Röse for the Primates and Marsupials (the teeth in the latter I have given reasons for regarding as milk-teeth); whereas in the development of $\underline{\text{m.}^{1}}$ of the Dog the Metacone develops before the Protocone of *that* tooth, in accordance with Taeker's results in the Ungulates.

A further difficulty is to be found in connection with the Metacone of the upper carnassial teeth of the Carnivora and with the Hypoconid of the lower. We have seen that two factors enter into the formation of both these cusps, namely, the Posterior Cingulum-cusp and the Secondary Cone, but they do

not always participate to the same extent. If, for instance, the carnassial teeth of the Tiger, Dog, and Bear be compared, this fact at once becomes apparent. And since I regard the Posterior Cingulum-cusp as a structure of greater antiquity than the Secondary cone, I conclude that the greater the share which the Posterior Cingulum-cusp takes in the formation of the Metacone, the earlier will that Metacone be developed, and *vice versâ*.

Such is, I believe, the explanation to be given of the somewhat varying results obtained by the aforementioned observers.

I have, I hope, said sufficient to indicate the main points of my Theory of Cingulum-cusp development. I do not say that there may not be many objections to it, but I think that it is, at any rate, free from serious ones.

The points in its favour may be thus summarized:—

(i.) It harmonizes more fully with what is known of the development of the teeth than either the Tritubercular or Multitubercular theory, the Primary cone representing the Reptilian cone and being always present.

(ii.) It is quite possible and easy thus to homologize the cusps of all teeth, except perhaps those derivative of the Multituberculate type.

(iii.) It is in accordance with Palæontological history.

(iv.) No supposed rotation of cusps is required to have taken place.

It is probable that in time, with greater knowledge and experience, many of the points of detail will have to be modified; indeed, I wish now only to give an outline of this hypothesis in order that it may be more generally tested. Great difficulty has been found in endeavouring to write a lucid explanation of this view, owing to the impossibility of homologizing the cusps under the old terminology.

In conclusion, I most gratefully express my thanks to Prof. G. B. Howes, not only for having suggested this subject for investigation, but also for having enabled me to carry it out in the Laboratory under his charge and for much kind advice and criticism. I would also express my thanks to Mr. G. L. Parsons, of the Westminster Medical School, for having made the drawings necessary for illustration of this paper.

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